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Art. XVIII.—*The Influence of the type of thickening on the rate of flow in models of Wood Vessels.*

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(With Plate XII).

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Introduction.

It is a well known fact that, in the conducting vessels of plants, various types of thickenings are present on the inner walls, and interest has centred in their function. These thickenings in the form of annuli, spirals, and networks, are of such a nature that they are preëminently suited to resist crushing forces (1).

They occur on the inner walls of the vessels through which the sap flows, and it is to be expected that they would exert some influence on the rate of flow of the sap, i.e., they would produce friction and introduce turbulent motion into the upward stream when it had sufficient velocity. Professor Ewart (2) has found that, owing to the presence of these thickenings and to the transverse walls, the flow of water through the capillary tubes of plants (viz., tracheae) is only about half what might be expected as calculated by Poiseuille's formula.

It was then thought that the different types of thickenings in the vessels might affect the rate of flow of the sap differently.

To test whether such different thickenings might have some relative effect on the rate of flow, the following experiments were carried out, using a model. This model was made to represent as closely as possible a wood vessel, magnified equally in all directions, but for practical reasons with the thickenings on a rod inside an outer tube, instead of on the inner surface as in a wood vessel.

The Apparatus.

Inside a glass tube (A) with an internal diameter of 2·3 cm. and 91 cm. in length, was fitted a solid glass rod (B) 1·9 cm. in diameter and 106 cm. in length. The glass rod was arranged so that it projected about 7·5 cm. at each end. After centring, the glass rod was fixed firmly in position, using wooden plugs, and the position of the plugs was scratched on the outer glass tube, so that they could always be placed in the same position on re-assembling the apparatus.

A rubber tube (C) was next fitted over one end of the outer glass tube, this being connected up with an aspirator (D) as shown in Figure 1.

On the other end of the glass tube another similar rubber tube with a glass tap was fitted. The positions where the rubber tubes fitted on were noted.

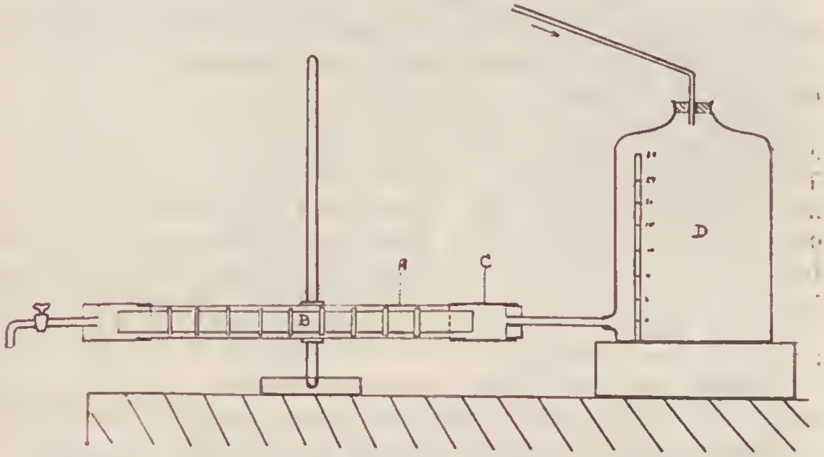


FIG. 1.—Diagram showing the arrangement of the apparatus.

The apparatus was then clamped in a horizontal position, so that every part of it was 6 inches above the level of the bench.

A second aspirator with a regulating tap was situated at 2 ft. 6 in. above the level of the bench. Water from this could be run into the first aspirator in order to maintain a constant level in the water there.

Method of Procedure.

In all the following experiments a stop watch was used to determine the time of flow of water through the tube, 60 seconds being the time in all cases. The temperature of the water flowing through the apparatus was taken at the beginning and end of a set of experiments, in order to correct for viscosity effects.

In most of the experiments difficulty was experienced in getting all the air out of the apparatus, i.e., from between the inner and outer tubes. This difficulty was overcome by first running methylated spirits rapidly through the apparatus and, following this by hot boiled water, passed through at a much slower rate. The remainder of the air left after running the alcohol through was dissolved out by the heated boiled water.

The velocity at which the water could be run through the apparatus was arranged for by using a series of "heads" of water in the first aspirator, viz., from a head of 33 cm. to a head of 1·2 cm., with 5 cm. and 2 cm. differences in level.

The volumes of water flowing through the apparatus in any set of experiments were measured in a large measuring jar.

Method of arranging the thickenings.

In the first attempts paraffin was used to introduce different types of thickening on to the inner tube. It was found impossible, however, to obtain a smooth surface on the paraffin, and consequently this method was abandoned.

Rubber banding of a size 1 mm. square in cross section was adopted for use for the spiral and annular types of thickening. The distance between the inner rod and the outer tube was 1·5 mm. on any particular side. When the rubber band was wound on, a space of 0·5 mm. was therefore left between the rubber band and the outer tube. The elastic band was fixed in position at each end by means of thin rubber bands. A specially made length of rubber tubing 1 mm. thick was used for the pitted and reticulate thickenings.

The type and arrangement of the thickenings as found in the vessels of the Cucumber stem served as a model on which the thickenings used in the experiment were based.

Camera lucida drawings were made of vessels showing different types of thickenings on their walls, and the distances apart of the thickenings in relation to the width of the vessel were measured, using a prepared scale. The ratio found was applied in working out distances between turns of the spiral, or the rings, in the model.

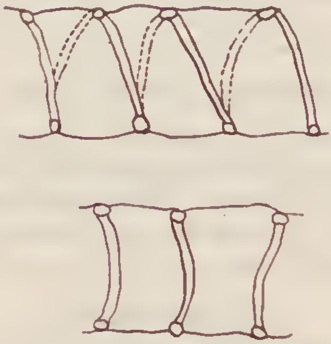


Fig. 2.
Camera Lucida drawings of wood vessels showing spiral and annular thickenings.—From a Cucumber stem.

In the case of the pitted and reticulate type of thickening, the procedure was adopted of working from rows of regularly arranged circular pits, through elongations of these to a reticulate condition. The different types of thickening used in each experiment are illustrated in Plate XII.

Experiment 1.—With no thickenings on the inner glass rod. Water was run through the apparatus for some time after all the air had been removed. Using the procedure above described, the results set out in the following table were obtained:—

Temp. of Water	Head of Water Cms.	Inches	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	13	29·10	22·00
	27·94	11	26·10	19·80
	22·86	9	24·30	18·26
	17·78	7	21·90	16·50
	15·24	6	19·60	14·84
	10·16	4	15·53	11·90
	7·62	3	13·93	10·40
	5·08	2	11·70	8·80
	2·54	1	9·10	6·80
	1·27	½	7·68	5·80

Estimation of the Linear Rate of Flow.—The volume of water contained in the cylindrical space between the rod (19 mm. diam.) and the tube (23 mm. diam.) in length of 55 cm. is 72 cc.

Volume of water flowing through in 1 second at 1·27 cm. head, 7·68 cc.

In 9·37 seconds 72 cc. will move a distance of 55 cm. Hence Linear Rate of Flow equals 5·8 cm. per second at a head of 1·27 cm. Linear Rate of Flow at other heads:

$$\frac{\text{Vol. of flow in 1 sec. at 1·27 cm. head}}{\text{Vol. of flow in 1 sec. at new head}} \times \frac{5·8}{1}$$

Experiment 2.—With spiral thickenings (Plate XII., Fig. 1). A rubber band 1 sq. mm. in cross section and 9 feet in length was wound on the inner glass rod, the turns of the spiral being placed 1·1 cm. apart and giving 46 turns over a length of 55 cm. This arrangement of the spiral was, as indicated earlier, modelled on a simple protoxylem type of spiral in a longitudinal section of a Cucumber stem. The diameter of the vessel was measured to the insides of the spiral thickenings, since this is the condition under which the present experiment is being conducted, i.e., the thickenings on the outside of a glass rod.

Diameter of vessel in Cucumber stem, 25 mm. Average distance apart of the turns of the spiral, 18 mm. Average width of band, 2 mm. Ratio of distance apart of the bands to the diameter of the vessel, 18:25.

Therefore spiral thickenings on the model should be set 1·30 cm. apart.

In the actual experiment the spiral was wound at distances of 1·1 cm. apart (46 turns), i.e., somewhat more closely spaced than is the case in the Cucumber vessel. The rod, bearing the bands in position, was then carefully placed inside the outer tube, centred and fixed there, using the wooden plugs. The apparatus was then connected up as described earlier.

After elimination of the air the following readings were made:—

Temp. of Water		Head of Water in cms.		Vol. in cc. per sec.		Linear Rate of Flow cms. per sec.
15°C	-	33·00	-	21·23	-	17·08
	-	27·94	-	18·90	-	15·30
	-	22·86	-	16·86	-	13·57
	-	17·78	-	14·75	-	11·87
	-	15·24	-	13·86	-	11·10
	-	10·16	-	11·43	-	9·18
	-	7·62	-	10·15	-	8·17
	-	5·08	-	8·30	-	6·78
	-	2·54	-	6·30	-	5·10
	-	1·27	-	5·30	-	4·27

Linear Rate of Flow.—Volume of rubber thickenings, 2·74 cc. Volume of water contained in a length of 55 cm., 69·26 cc. Linear rate of flow at 1·25 cm. head, 4·27 cm. per sec.

Experiment 3.—With an increased number of spiral thickenings. The number of spiral turns was increased to 114 in this

Temp. of Water		Head of Water in cms.		Vol. in cc. per sec.		Linear Rate of Flow cms. per sec.
15°C	-	33·00	-	18·20	-	15·10
	-	27·94	-	16·50	-	13·60
	-	22·86	-	14·46	-	12·00
	-	17·78	-	12·70	-	10·60
	-	15·24	-	11·60	-	9·70
	-	10·16	-	8·50	-	7·00
	-	7·62	-	7·13	-	5·90
	-	5·08	-	5·80	-	4·20
	-	2·54	-	3·75	-	3·10
	-	1·27	-	3·35	-	2·80

experiment, and they were wound on at distances of 4 mm. apart. This was modelled on an older vessel in the Cucumber stem which was showing a more closely wound spiral.

Volume of rubber thickenings, 6·8 c.c.

Experiment 4.—With spiral thickenings doubly wound. A double wound spiral, such as is found occurring in the larger

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	19·30	16·00
	27·94	18·00	14·90
	22·86	16·10	13·30
	17·78	14·20	11·76
	15·24	12·90	10·70
	10·16	9·97	8·26
	7·62	8·43	7·00
	5·08	6·90	5·70
	2·54	5·13	4·25
	1·27	4·10	3·40

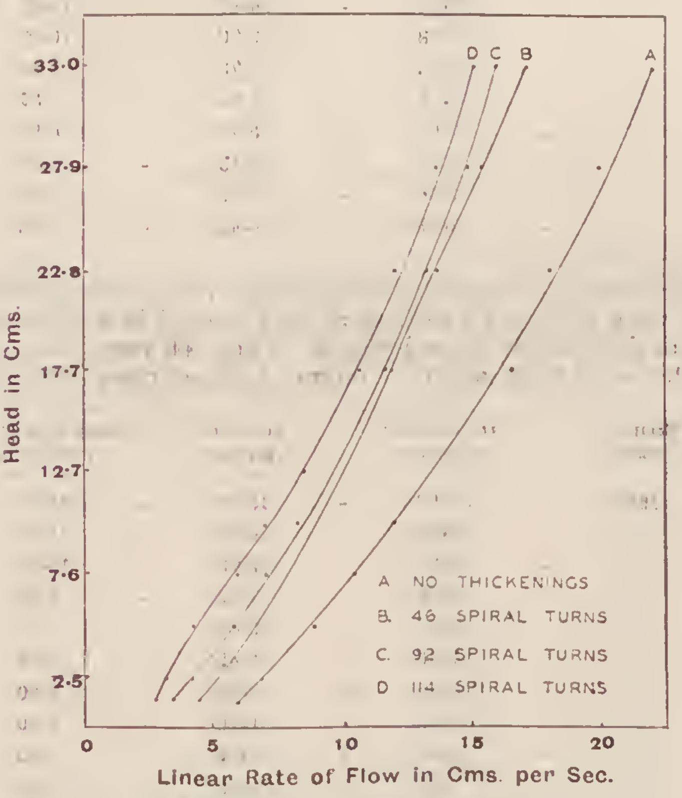


FIG. 3.—The effect of Spiral thickenings on the rate of flow.

vessels of the xylem in the Cucumber stem, was used in this experiment. Two separate spirals of 46 turns each were wound on so that the distance between any two turns of the spirals was 4·7 mm. The spacing here approximates very closely to that found in the Cucumber vessels. The volume of the rubber thickenings was 5·48 cc.

Experiment 5.—With annular thickenings (Plate XII., Fig. 2). The 9 feet of rubber band used in a previous experiment (46 spirals) was cut up and made into 35 rings of a size large enough to make a tight fit on the inner glass rod, and these were spread over 55 cm. at distances of 1·5 cm. The spacing here approximated very closely to the relative spacing of the annular thickenings in the Cucumber vessel. Volume of rubber rings, 2·74 cc.

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	17·20	13·66
	27·94	15·55	12·35
	22·86	14·40	11·43
	17·78	12·70	10·09
	15·24	11·78	9·34
	10·16	9·90	7·85
	7·62	8·75	6·94
	5·08	7·13	5·66
	2·54	5·33	4·21
	1·27	4·45	3·54

Experiment 6.—With increased number of annular thickenings. These were increased to 46, so as to be equal in number to the turns of the spiral in Experiment 2. These 46 rings were spaced at distances of 1 cm. apart. Volume of rubber rings 3·59 cc.

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	15·40	12·37
	27·94	14·05	11·30
	22·86	12·78	10·27
	17·78	11·22	9·01
	15·24	10·45	8·41
	10·16	8·45	6·78
	7·62	7·46	6·00
	5·08	6·20	5·00
	2·54	4·72	3·90
	1·27	3·90	3·14

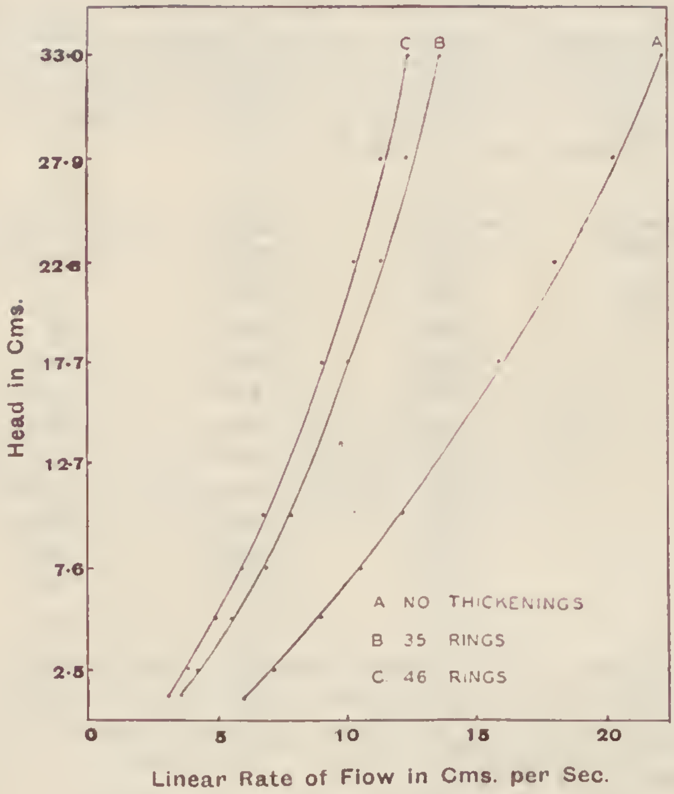


Fig. 4.—The effect of Annular thickenings on the rate of flow.

Experiment 7.—With solid rubber tube (Plate XII., Fig. 3). In this experiment a solid rubber tube 1 mm. thick and 55 cm. long was fitted on to the inner glass rod. Volume of rubber thickening, 39 cc.

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	15·78	26·33
	27·94	14·23	23·77
	22·86	12·50	20·87
	17·78	10·45	17·46
	15·24	9·45	15·76
	10·16	6·91	11·54
	7·62	5·75	9·60
	5·08	4·37	7·28
	2·54	3·23	5·37
	1·27	2·55	4·26

Experiment 8.—With rubber tube pitted (Plate XII., Fig. 4). Circular pieces of rubber 3 mm. in diameter were cut out of the solid rubber tube, giving a pitted appearance when placed on the glass rod. The pits were arranged in five rows of 18 each, spread over the length of 55 cm. The volume of the rubber thickening was now 38·37 cc.

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	13·07	21·50
	27·94	11·60	19·06
	22·86	10·10	16 59
	17·78	8·66	14·23
	15·24	7·80	12·80
	10·16	5·90	9·70
	7·62	4·93	8·08
	5·08	3·81	6·26
	2·54	2·50	4·10
	1·27	1·85	3·04

Experiment 9.—With double number of pits in rubber tube (Plate XII., Fig. 5). The number of pits cut in the solid rubber were doubled for this experiment, and were made to alternate in position with the other 90 pits. The volume of the rubber thickenings was 37·74 cc.

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	11·98	19·17
	27·94	10·55	16·86
	22·86	9·03	14·43
	17·78	7·63	12·20
	15·24	6·73	10·76
	10·16	5·05	8·08
	7·62	4·00	6·40
	5·08	3·00	4·78
	2·54	2·07	3·30
	1·27	1·55	2·48

Experiment 10.—With round and elongated pits in rubber tube (Plate XII., Fig. 6). A number of the pits (104) in the rubber were enlarged to form an elliptic area, while the other pits (74) were left as before. The volume of the rubber thickening was 34·38 cc.

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	12·98	19·00
	27·94	11·50	16·83
	22·86	10·13	14·82
	17·78	8·75	12·80
	15·24	8·13	11·88
	10 16	6·10	8·94
	7·62	5·05	7·38
	5·08	3·70	5·40
	2·54	2·43	3·54
	1·27	2·05	3·00

Experiment 11.—With elongated pits in rubber tube (Plate XII., Fig. 7). All the pits in the rubber tube were cut to an elliptic shape, giving a thickening approaching to a reticulate type. Volume of rubber thickening, 30·43 cc.

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	13·81	18·22
	27·94	12·20	16·11
	22·86	10·61	14·00
	17·78	8·95	11·83
	15·24	8·05	10·63
	10·16	6·00	7·90
	7·62	4·75	6·25
	5·08	3·75	4·96
	2·54	2·83	3·73
	1·27	2·21	2·92

Experiment 12.—With reticulate thickening (Plate XII., Fig. 8). The rubber tube on the glass rod was further cut away for this experiment, so the thickenings left were of a pronounced reticulate character. Volume of rubber thickening, 19 cc.

Temp. of Water	Head of Water in cms.	Vol. in cc. per sec.	Linear Rate of Flow cms. per sec.
15°C	33·00	13·45	14·03
	27·94	12·03	12·55
	22·86	10·11	10·57
	17·78	8·70	9·07
	15·24	7·83	8·18
	10·16	6·13	6·40
	7·62	5·06	5·28
	5·08	4·05	4·23
	2·54	2·85	2·96
	1·27	2·25	2·35

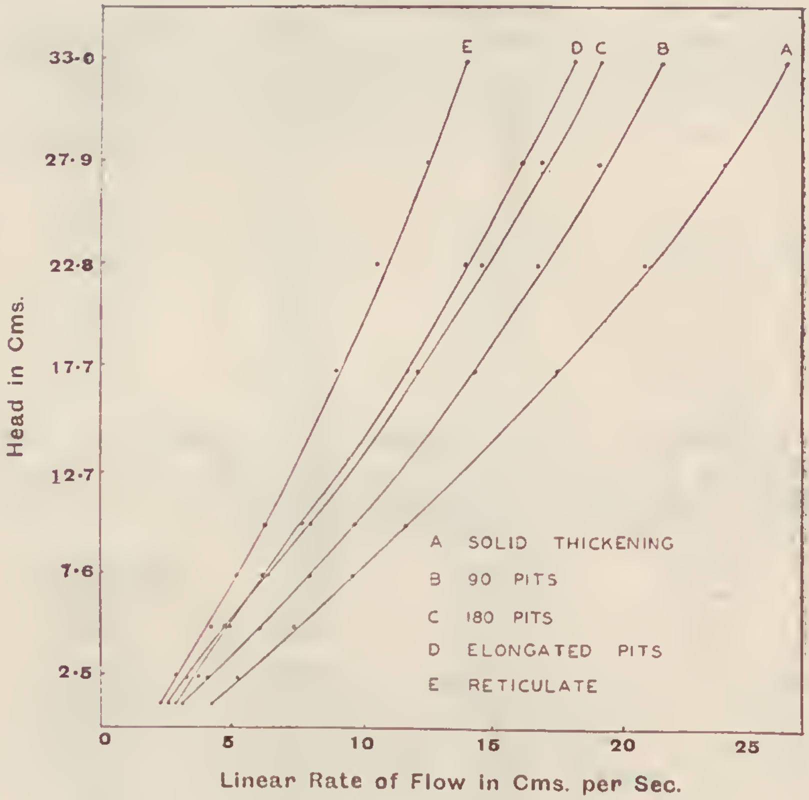


FIG. 5.—The effect of Pitted and Reticulate thickenings on the rate of flow.

Discussion of Results.

An examination of the graphs plotted from the results of Experiments 1, 2, and 3 shows that the introduction of spiral threads into a cylindrical channel has a marked effect on the rate of flow of water through such a space, but this retardation is still more marked when a corresponding number of annular rings are introduced (See Fig. 6). This difference, particularly with high rates of flow, can be attributed to eddy currents forming at each ring, whereas with a spiral thread the flow tends to follow a spiral path. The spiral thread increases the distance the liquid must travel in order to pass through the tube, but the resistance to flow is not increased to the same extent as with the formation of eddy currents. The greater the number of annular rings the greater is the resistance to flow, but the proportional increases decrease as the total number of rings increases.

Two parallel spiral threads increase the resistance to flow only to a slight extent as compared to a single spiral thread, since there are merely two spiral channels of water current instead of one twice the breadth. A single spiral wound with nearly three times the number of turns gives a greater resistance than one a third of its length, but the increased resistance is much less than one would expect. In addition, at intermediate heads, all the curves seem to approximate, for what reason it is difficult to say.

The pitted type of thickening allows a greater rate of flow at high heads than do the annular or spiral, but in all cases the rate of flow at a low head is below that of the annular and spiral types.

It is noticeable that the rate of flow drops very considerably when the first 90 pits are cut out of the solid rubber, but that the addition of a second series of alternating pits does not affect the rate of flow to the same extent.

The first big drop occurs because of the change from stream line flow to turbulent flow. The addition of the next 90 alternating pits serves to decrease the rate of flow to a slight degree, because

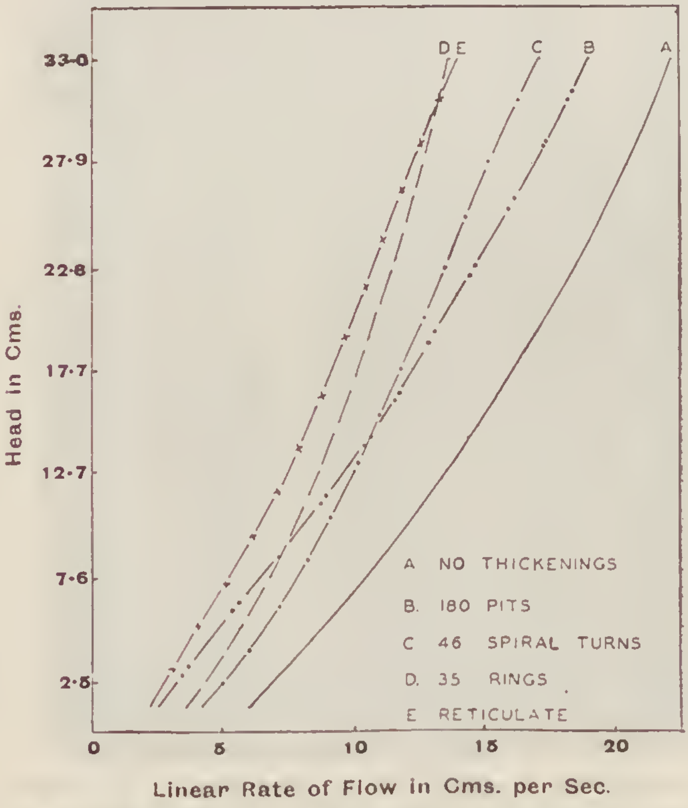


FIG. 6.—Comparison of the effect of Spiral, Annular, Pitted and Reticulate thickenings on the rate of flow.

of the further breaking up of the stream of water, and the formation of eddy currents round the new pits. In these pitted types we get a serpentine flow of the water between the pits. Eddy currents are only formed in the vicinity of these pits, and the rate of flow is not affected to so great an extent at a high head as with the annular thickenings.

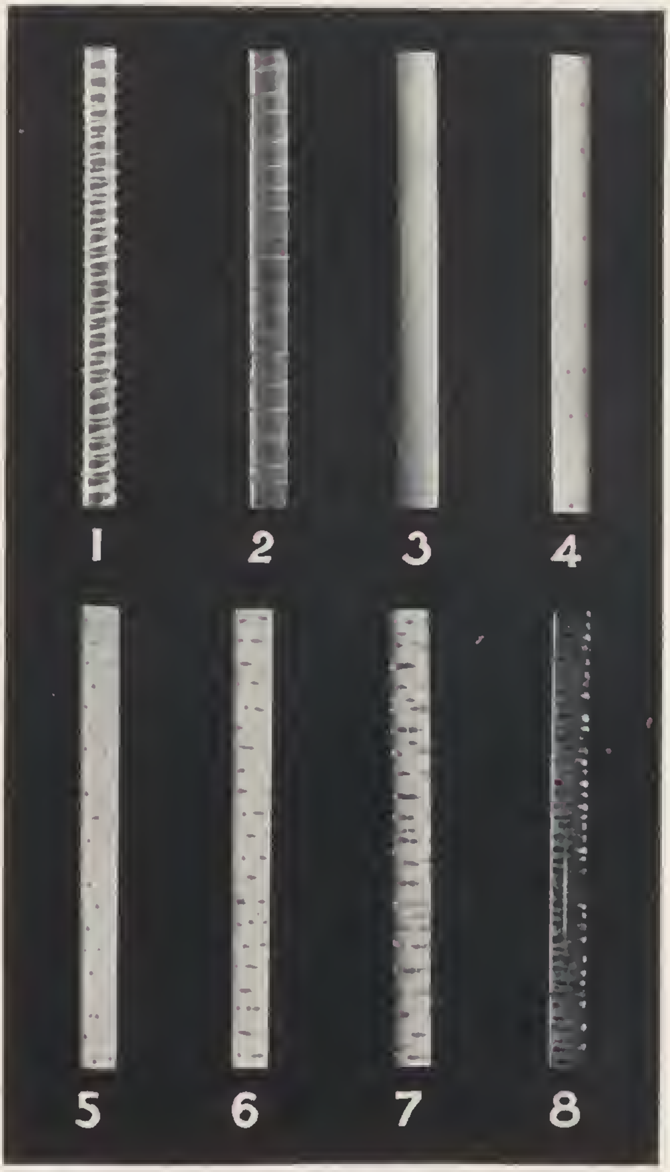
With the extreme reticulate type of thickening the rate of flow is greatly retarded, giving values at a head of 33 cm. which are very close to those obtained for the annular type of thickening at a similar head. At a head of 1·27 cm. the reticulate thickening gives the greatest retardation of flow for the whole series of experiments. Eddy currents exercise a great effect in this case, and are more in evidence at low heads for reticulate thickenings than they are for similar heads using annular thickenings.

Conclusions.

The results of these experiments indicate that in models of wood vessels the rate of flow of the water in general is lowest when reticulate thickenings are used. The annular type exercises the next greatest effect, followed by the pitted type. At heads above 10 cm. the spiral thread has a more pronounced effect on the rate of flow than has the pitted type, but otherwise spiral thickenings least retard the rate of flow. Since all the above types of thickening occur in the wood vessels of plants it is reasonable to assume that they would exercise a similar relative effect on the rate of flow of the sap in the vessels.

A biological explanation of the type of thickening occurring in wood vessels is possible. Annular vessels are developed early and they require a minimum amount of thickening material. They are highly flexible, and since they develop early in thin walled tissue, there is no danger of their being occluded by the pressure of surrounding harder tissues. Annular vessels are narrower than the vessels of the metaxylem, and may be expected to offer greater resistance to flow. Spiral vessels also develop early, and these offer less resistance to flow. As the pressure of the surrounding tissues increases, the plant develops closer spirals and finally reticulate or dotted vessels which are comparatively rigid. As the conducting area is now larger the resistance to flow is a factor of less importance than is rigidity. The higher resistance to flow in reticulate vessels at low heads as compared with spiral vessels is also far more than made good by their increased diameter. At low heads diameter is far more important than the character of the internal surface.

In conclusion, I would like to acknowledge the helpful suggestions and criticisms from Professor Ewart during the progress of the work.



B.J.G. photo

Types of Thickenings in Wood Vessels.